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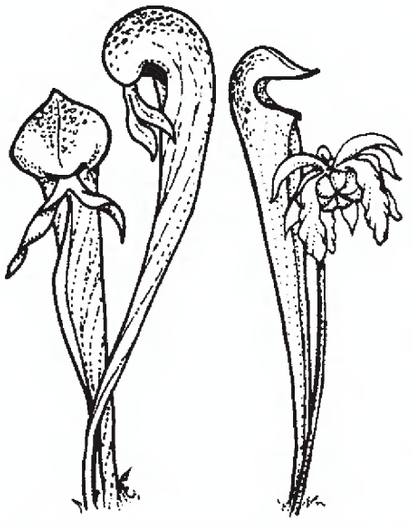

CARNIVOROUS PLANT NEWSLETTER

Journal of the International Carnivorous Plant Society
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Front Cover: *Drosera schizandra* on the bank of a disused logging trail, Mount Bartle Frere, North Queensland. Photo by Greg Bourke. Article on page 92.

Back Cover: *Drosera adelae* can attain red coloration when grown in full sunlight, here seen growing in rocks near a waterfall, Abergowrie, North Queensland. Photo by Greg Bourke. Article on page 92.

Carnivorous Plant Newsletter is dedicated to spreading knowledge and news related to carnivorous plants. Reader contributions are essential for this mission to be successful. Do not hesitate to contact the editors with information about your plants, conservation projects, field trips, or noteworthy events. Advertisers should contact the editors. Views expressed in this publication are those of the authors, not the editorial staff.

All correspondence regarding dues, address changes and missing issues should be sent to the Membership Coordinator at the ICPS. Do not send such correspondence to the editors. Checks for subscriptions should be made to the International Carnivorous Plant Society in US funds. Dues, including a subscription, are $30 per year.

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International Carnivorous Plant Society (ICPS) Treasurer

The ICPS seeks to fill an opening on the board of directors for the position of Treasurer. The successful candidate will have experience with small business accounting and banking as well as experience with carnivorous plants. Experience with non-profit organizations and/or international charity is desirable. The duties include monitoring e-mail notifications of financial activity on a daily basis, paying bills, preparing financial statements and yearly budget, working with our accountant to file the California and Federal income tax returns, and assisting the Membership Secretary and Store/Seedbank Manager with payment issues. Candidates should be responsive, meticulous, organized, a permanent resident of the United States, and live near a Chase Bank branch. Experience with Quickbooks or similar accounting software is a plus. Board meetings are via Skype and typically occur once a quarter in the evening (US time zones).

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An account of *Drosera* section *Prolifera*

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Introduction

The species that comprise *Drosera* section *Prolifera*, *Drosera adelae*, *D. prolifera*, and *D. schizandra*, or as commonly known, "The Three Sisters", are endemic to Far North Queensland. They are unique to the genus in that they are found growing exclusively in rainforest habitat. Over the past 8 years the authors have made four separate field trips to observe these unusual and uncommon *Drosera*. The literature published to date on these taxa is general, often based on observations of cultivated plants. One can easily form the superficial view that they grow relatively close to each other in similar micro-habitats, it is only when herbarium sheets, field observations, and personal accounts are scrutinized that a different story emerges. The objective of this account is to show the broad area these species occur and to highlight the similarities and differences in their micro-habitat. Australia is a vast continent and the area that these species inhabit is approximately a 400 km stretch of hinterland that runs roughly parallel to the coast from Townsville, north to Cape Tribulation.

Taxonomy, Distribution and Habitat

(adapted from, Lowrie 2014 and Lowrie *et al.* 2017 and annotated with the author's field observations)

Drosera section *Prolifera* C.T.White
Publication: Victorian Naturalist 57: 94-95 (1940).

Type species: *Drosera prolifera* C.T.White

Plants perennial; hairy-rooted; leaves erect to semi erect, together forming an open, leafy rosette; lamina when mature, reniform, lanceolate or obovate; stipules red, reduced to 2 small trichomes attached to base of petiole on upper side; styles 3 or 4, terete, reddish in lower half, white above, bilobed at apex to form a ± Y-shape configuration, each free lobe apex truncate; stigmas white, simple, at the tips of each spreading lobe, papillose.

Key to *Drosera* section *Prolifera*

1a: Plant with an open rosette of erect and semi erect leaves 2
1b: Leaves in a rosette 3

2: Leaves narrowly lanceolate ..... *Drosera adelae*

3a: Leaf lamina reniform ..... *Drosera prolifera*
3b: Leaf lamina obovate ..... *Drosera schizandra*

Figure 1: *Drosera adelae* in shaded conditions near Cardwell, North Queensland (left; photo by Greg Bourke). Flower at same location (right; photo by Richard Nunn).

Drosera adelae F.Muell. (Fig. 1; Back Cover)
Publication: Fragmenta Phytographiae Australiae 4(30): 154, t. XXXIII (1864).
Type location: Dalrymple's Creek, Rockingham Bay

Etymology

The epithet *adelae* is possibly derived from "Adelae de L'Arbre", or the genitive singular of Adela, a Latinized form of Adele. The identity of the lady in question is unknown (Australian Plant Census).

Distribution

Drosera adelae is endemic to Queensland. Its range extends from Rockingham Bay, Hinchinbrook Island, Cardwell, Abergowrie to Kennedy. Additional sub-populations have been documented in the extensive Walter Hill Range, particularly Tully Gorge National Park.

Habitat and Field Notes

This species grows in the foothills of mountains along the sandy banks of creeks, seeps, among rocks and the splash zones of waterfalls, it also follows creek lines into the coastal plains. *Drosera adelae* is a relatively widespread species of the lowlands, but highly localized. This may be because *D. adelae* tolerates a broader range of conditions; it can be found by waterfalls in full sun, through to dark, closed-canopy rainforest but always associated with areas that remain wet well into the dry

season. Plant coloration may be related to exposure to light, those in brighter conditions producing more red pigmentation, however observations of cultivated plants from several locations indicate there may also be genetic variation (G. Bourke pers. obs).

Site 1: Waterfall, Kennedy, North Queensland

A short drive up an old disused road in the hills behind Kennedy to an elevation of 500 m. The plants were observed growing in rock crevices in the spray zones of a perennial waterfall. At various times of the day the plants are exposed to full sun.

Site 2: Creek crossing, Bruce Highway, Cardwell area, North Queensland

Along the Bruce Highway at various intervals, creeks, fueled by water from the rainfall in the hinterland, make their way to the ocean. In some of these creeks *Drosera adelae* can be found growing on the banks in peaty sand. Dense populations thrive in the permanently wet, shady, and warm conditions. Mosquitos and ants are abundant, making field observations an uncomfortable experience. In most years these creeks are constantly in flow, however it has been observed in the driest years that there is no water and the plants recede to fleshy roots.

Description (Lowrie 2014)

A fleshy, hairy-rooted perennial herb with a loose, open rosette. Stem 2-10 cm tall, generally 1.5-2 mm diameter. Leaves in the early stages of growth erect and circinate, becoming horizontal with age, spent leaves lying prone around the basal portion of the stem. Juvenile leaves are obovate, subsequent leaves narrowly elliptic, and mature leaves lanceolate, alternately arranged in a spiral along the stem. Petiole short, almost sessile and glabrous. Lamina 10-25 cm long, 7-10 mm wide, with a raised longitudinal midrib on both surfaces along its entire length. Inflorescence a terminal, one-sided helicoid cyme, 25-35 cm long, many-flowered. Peduncle and pedicels covered with scattered sessile glands and scattered wispy pilose hairs. Pedicels 5-6 mm long, semi-erect and lengthening in fruit. Flowers 0.6-0.8mm in diameter, red, reddish orange or cream, petals broadly lanceolate, margins entire, 2.5-3.5 mm long, 0.3-0.4 mm wide at the base, dilated to 1.2-1.5 mm wide near the center, then abruptly narrowing to 0.5-0.6 mm wide and forming an acuminate apex. Sepals green, lanceolate, 2-2.5 mm long, 0.5-0.6 mm wide at the base, dilated to 0.8-0.9 mm wide near the center, then quickly narrowing to 0.3-0.4 mm wide and forming a long acuminate apex, margins and apex entire, abaxial surface glabrous. Stamens 5, each 4-4.5 mm long, the filaments and anthers white, bi-lobed and reddish at the apex, the pollen creamy white, or yellow in the red flowered forms. Ovary green or reddish, subglobose, 0.9-1 mm long, 1-1.5 mm diameter. Styles 3 or 4, rust-orange at the base, white at the apex, 0.6-0.7 mm long, 0.1-0.15 mm in diameter, bi-lobed at the apex and forming a T-shape with each free lobe, 0.4-0.5 mm long, curved along its length. Stigmas white, simple, located at the tips of the free paired lobes, papillose, style-stigmas positioned horizontally from the apex of the ovary.

Phenology

This species flowers from June to November. It is capable of perennating through adverse conditions by retreating to its fleshy roots, as happens at locations within its range that dry out completely during the dry season. Whilst self-fertile, *Drosera adelae* often forms large clonal colonies through the formation of plantlets along its roots and rarely from its leaves. It is also capable of producing plantlets directly from its flowers in a similar manner to *D. prolifera*.

Figure 2: *Drosera prolifera*, Noah Creek, North Queensland (left; photo by Greg Bourke). Flower of cultivated *Drosera prolifera* (right; photo by Greg Bourke).

Drosera prolifera C.T.White (Fig. 2)
Publication: The Victorian Naturalist 57(5): 94-95 (1940).
Type location: Cook District: Thornton Peak (in sheltered places near the summit) alt. 4000 ft.

Etymology

The epithet *prolifera* is from the Latin *proles* (offspring) and *fero* (to bear), a reference to the ability of this species to produce offshoots, usually arising from the inflorescence.

Distribution

Drosera prolifera is endemic to North Queensland. It is recorded from the summit and flanks of Thornton Peak and a small number of watercourses draining from that mountain.

Habitat and Field Notes

This species grows in rainforest areas among rocks and on sandy banks along creeks occasionally flooded by monsoonal rains. The ability of *Drosera prolifera* to produce additional plants on every flowering peduncle ensures that crowded colonies of plants are quickly formed in suitable sites.

Site 1: River embankment, Noah Creek, North Queensland

A difficult 3-hour walk up a branch of Noah Creek. Initial part of the walk required struggling through rainforest filled with Rattan (*Calamus muelleri*) and Screw Pine (*Pandanus tectoris*) and

the odd Cassowary nest, followed by 2 hours of climbing over progressively larger boulders, some reaching the size of a small house. Plants were observed on a small moss-covered embankment, forming dense colonies in partially shaded rainforest habitat. Plants grew down to the water's edge and at time of higher rainfall would have been inundated.

Site 2: Thornton Peak, North Queensland

Although the authors did not visit the type location, it is worthy of including notes from others as the habitat and conditions are clearly different at this higher elevation. Plants found at and near the summit of Thornton Peak, on moist rock ledges. The vegetation at this elevation, although rainforest, is more open and stunted than at lower elevations. Rainfall is 10 m per year and the weather is cooler and more unpredictable than lowland areas.

Description (Lowrie 2014)

A green, fleshy, hairy-rooted, perennial herb with a small number of erect to semi-erect active leaves, together forming an open leafy rosette up to 6-8 cm in diameter, leaves erect at first, then semi-erect and later flat on soil surface to make way for new, central leaves. Flowering peduncles long, lateral, positioned just above soil surface, peduncles similar to strawberry plant runners in that they produce additional plantlets at their tips after flowering, thus producing crowded colonies of individual plants. Lamina when mature, reniform, 20-25 cm long, 22-27 mm wide, adaxial surface with clear white or red tipped insect-catching glands positioned around margins and smaller red tipped glands within, abaxial surface glabrous; petiole 2-4.5 cm long, 2.5-3 mm wide, semi lenticulate in section, with a longitudinal rib on adaxial surface, dilated a little at base, glabrous. Stipules red, reduced to 2 small trichomes attached to base of petiole on upper side. Inflorescence peduncles 1 to 4, 18-20 cm long, producing a vegetative shoot at its apex after anthesis, flowers 4 to 8, widely-spaced; pedicels curved, 3-5 mm long; bracts linear, 1-2 mm long, opposite and slightly below pedicel, fruiting peduncles almost prostrate. Sepals beige, lanceolate, 0.8-0.9 mm wide at base, dilated to 1-1.2 mm wide just above center, then quickly narrowing to 0.3-0.4 mm wide and forming long ± sharp, but gnawed acuminate apex, 3.5-4 mm long, margins entire, abaxial surface glabrous, in face view apices positioned within corolla at angles of a perfect pentagon shape, each sepal perfectly positioned between petals. Petals adaxial and abaxial surfaces reddish purple, obovate, 0.5-0.55 mm wide at base, dilated to 1.8-2 mm wide near apex, 2.2-2.5 mm long, margins entire, apex crenate. Stamens 5, 1-1.2 mm long; filaments dilated in upper half, white in lower half, reddish above; anthers and pollen white. Ovary reddish, broadly obovoid, 1.2-1.5 mm long, 1.2-1.5 mm in diameter at anthesis, glabrous. Styles 3 or 4, terete, reddish in lower half, white above, 0.8-0.9 mm diameter, 0.6-0.7 mm long, bilobed at apex to form a ± Y-shape configuration, each free lobe, 0.4-0.5 mm long, apex truncate. Stigmas white, simple, at tips of each spreading lobe, papillose, Styles positioned horizontal from apex of ovary. Seeds dark brown to black (mainly black), ± an ovoid to obovoid shape, sides irregular distorted in and out slightly, 0.53-0.63 mm long, 0.35-0.4 mm in diameter, apical pole often narrowing, apically truncate, funicle positioned proud of basal pole, 0.013-0.015 mm long, 0.01-0.013 mm in diameter, surface deep irregular reticulate-alveolate honeycomb-like cells, cell ridges smooth and undulating.

Phenology

This species flowers all year round. Plants may die back to their fleshy roots if habitats dry out in the dry season.

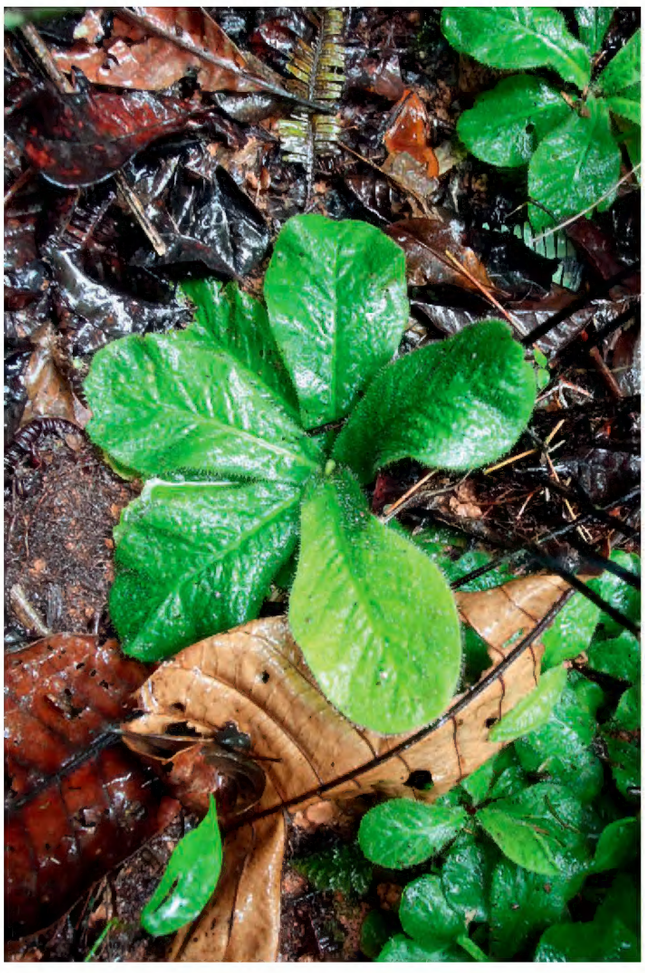

Figure 3: *Drosera schizandra* grows the largest rosettes of all *Drosera*, Mount Bartle Frere, North Queensland (left; photo by Greg Bourke). *Drosera schizandra* in bloom, Mount Bartle Frere, North Queensland (right; photo by Richard Nunn)..

Drosera schizandra Diels (Fig. 3; Front Cover)
Publication: Das Pflanzenreich 26: 80 (1906).
Type location: Queensland. North Queensland, Mount Bartle Frere

Etymology

The epithet *schizandra* is from the Greek *schistos* (divided) and *andrus* (male), in reference to the divided anthers of this species.

Distribution

Drosera schizandra is endemic to Queensland, where it is known only from the rainforest covered lower slopes of Mount Bartle Frere.

Habitat and Field Notes

This species grows in rainforest at an altitudinal range of 300-600 m. in areas among rocks in deep shade, and in damp sand along the banks of streams. Large, mostly clonal colonies exist along some of the old logging trails on the lower slopes of Mount Bartle Frere. Plantlets form along exposed roots, while broken leaves occasionally produce plantlets in the wet season. *Drosera schizandra*, *D. adelae* and *D. prolifera* grow in similar rainforest habitats. However, of the three, *D. schizandra* favors the darkest, most shady habitats.

Site 1 and 2: Logging Trail, Mount Bartle Frere, North Queensland

Although only about 80 km from Cairns, Mount Bartle Frere, takes about 2 hours to drive from Cairns. A 45-minute walk along a disused logging trail covered in Rattan, Pandanus and wild Strawberry, with copious leeches. The first site is a small embankment in near total shade, yielding a dense colony of plants growing in sandy clay. Plants range in size up to a dinner plate in diameter. Further along the trail, a much larger colony of plants was found growing in more sun but still in rainforest habitat. The plants had colonized the disturbed and exposed embankment cutting along the side of the trail. Warm days and cool nights are experienced at this intermediate elevation.

Site 3: River edge, Mount Bartle Frere, North Queensland

Along the same trail a few hours more walking down to approximately 300 m, the trail finishes at a fast-flowing river. *Drosera schizandra* was observed growing amongst the rocks in moist sand. These plants were smaller and more exposed to the elements than those at the previous 2 sites.

Description (Lowrie 2014)

A large, fleshy-rooted perennial herb with a few-leaved rosette 16-20 cm in diameter, each leaf varying in length and width, mature leaves semi-erect and adpressed to the soil. Lamina when mature obovate, 8-10 cm long. 4-5 cm wide, entire except irregularly crenate apex and commonly a little emarginate, mid vein prominently raised on adaxial and abaxial surfaces, with additional venation branching outwards from mid vein on both surfaces, but prominently raised only on abaxial surface, adaxial surface covered with long, translucent white trichomes with red-tipped glands, abaxial surface sparsely hirsute, hairs mainly along raised midrib and lateral veins. Juvenile leaves distinctly petiolate; mature leaves sessile or very shortly petiolate; stipules laciniate, attached to base of petiole on upper side; petiole semi-terete in section, 2-2.5 mm in diameter. Inflorescence 1, peduncle 12-14 cm long, 10-25-flowered, arising from center of rosette; peduncle and pedicels covered with non-glandular hairs; pedicels 5-10 mm long. Bracts linear 2.7-3 mm long. Sepals greenish, lanceolate, 4-5 mm long, 0.9-1 mm wide at base, dilated to 1.6-1.8 mm wide just above center, then narrowing towards apex, margins entire in its lower parts, irregularly serrate in upper parts, with a deeply serrate apex, abaxial surface covered with non-glandular hairs. Petals adaxial and abaxial surfaces a very dark reddish purple, obovate, 1.5-2 mm wide at base, dilated to 4-5 mm wide near apex, 5.5-6.5 mm long, margins entire, apex crenate. Stamens 5, red; filaments V-shaped, base leg dilated in middle, 1.3-1.5 mm long, apex bilobed and reflexed, 0.9-1 mm long; anthers and pollen yellow, positioned on underside of reflexed apical lobes of filament. Ovary red, obovoid, 1.2-1.5 mm long, 1.1-1.4 mm in diameter at anthesis; carpels 3, bilobed, glabrous. Styles 3, terete, red, 0.9-1 mm long, semi-erect, bilobed, lobes curved and reflexed a little, each lobe with 1-3 white stigma lobes. Stigmas papillose. Seeds unknown.

Phenology

This species flowers from November to July. Although a rare event, it can retreat to its fleshy roots if its habitat dries out in the dry season.

Discussion

Drosera adelae, *D. prolifera*, and *D. schizandra*, although differing morphologically, especially in terms of their leaf shape, appear to have evolved from a common ancestor, they have similar floral parts; the stamens and receptive styles are prominently displayed at anthesis because the petals fully

Table 1: Micro-habitat observations of *Drosera* section *Prolifera* sites.

	Drosera adelae site 1	*Drosera adelae* site 2	*Drosera prolifera* site 1	*Drosera prolifera* site 2*	*Drosera schizandra* site 1 & 2	*Drosera schizandra* site 3
Elevation	20 m	500 m	100 m	1300 m	600 m	300 m
Substrate	sandy peat	accumulated organic matter in rock crevices	moss growing over granite	sand in sheltered areas along rock faces	sandy clay	moist sand
Light	50% shade	bright light	50% shade	50% shade	deep shade	50% shade
Moisture	normally constant but can dry out in extreme drought	year-round moisture from waterfall.	constant, fed by seeps	constant, fed by seeps	very wet in rainy season, dryer in winter months	access to year-round moisture from proximity to river
Growth cycle	can die back to roots in drought	year-round	year-round	year-round	year-round	year-round

* the authors were unable to visit the type location for *Drosera prolifera* on the summit of Thornton Peak and hence have relied on literature and personal accounts for the data in the table.

reflex. The anthers, being on the underside of the exposed reflexed lobes of the stamens, shelter the pollen grains from the frequent, heavy rains. In addition to these floral similarities, all have chromosome counts of 2n = 30, as well as similar seedling characteristics that indicate a close relationship (Lowrie 2014).

Conclusion

The fieldwork undertaken in conjunction with a detailed literature and herbarium review provides the following conclusions

1. The species in *Drosera* section *Prolifera* are closely related and have evolved from a common ancestor, although they are now morphologically quite different.
2. All three taxa inhabit rainforests, however their micro-habitats are different, with *Drosera adelae* being a tropical lowland species, *D. schizandra* preferring more shade at elevations ranging between 300-600 m, and *D. prolifera* being predominantly a montane species occurring on the summit of Thornton Peak at 1300 m, but with isolated populations close to sea level.
3. Although endemic to Far North Queensland, each species is geographically isolated, and they never co-occur.

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Quantification of growth benefit of carnivorous plants from prey

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Keywords: Cost-benefit relationships, mineral cost and benefit, stimulation of root nutrient uptake, growth benefit.

Abstract: The growth of carnivorous plants is usually limited or co-limited by shortage of available mineral nutrients N, P, and K in barren soils or waters. Carnivorous plants capture animal prey, absorb mineral nutrients from digested prey, and partly overcome the nutrient limitation. Therefore, prey capture leads invariably to marked and significant growth increase as the main ecophysiological benefit of carnivory. Here, a novel functional-ecological approach of how to quantify growth benefit efficiency of carnivory is explained. It expresses plant growth increase due to prey catching or feeding per amount of N or P or K theoretically absorbed from prey (or applied in mineral solution onto the traps) in growth experiments.

Introduction

Carnivorous plants (CPs) usually grow in soils and waters poor in available mineral nutrients (N, P, K, Ca, Mg) and, at least in terrestrial species, their foliar or shoot N, P, or K contents are on average somewhat lower than those in non-CPs (e.g. Juniper *et al.* 1989; Adamec 1997, 2011; Ellison 2006). Therefore, their natural or greenhouse growth is usually limited or co-limited by shortage of N, P, and K in their organs (Ellison & Adamec 2011). Carnivorous plants capture animal prey (mostly arthropods), absorb mineral nutrients from digested prey, and partly overcome the nutrient limitation. Consequently, prey capture leads invariably to marked and significant growth increase as the main ecophysiological benefit of carnivory. However, animal prey is a relatively rich source only for N and P as their tissue contents in typical preys (per unit dry weight, DW) are 5-10 times higher than those in CP shoots, but the tissue K, Ca, and Mg contents in preys are comparable with those in plants or lower. Therefore, CPs can cover commonly >50% of their seasonal N and P gain from carnivory, but only around 1-5% of K, Ca, or Mg (Adamec 1997, 2011).

It has been found for various *Drosera* and *Pinguicula* species that prey capture leads to a marked stimulation of mineral nutrient uptake by roots; the same effect is also attained if drops of a mineral nutrient solution are applied onto the traps (Hanslin & Karlsson 1996; Adamec 1997, 2002, 2011). The amount of mineral nutrients (N, P, K, Ca, Mg) absorbed consequently by stimulated roots *minus* unfed controls can be ca. 1.6-27 times higher than that directly absorbed from prey carcasses or nutrient solution. It characterizes the efficiency of the use of foliar nutrient uptake for mineral nutrient uptake by roots in total plant biomass (Adamec 2002, 2011). Yet the physiological nature of this root uptake stimulation remains unknown.

As introduced by Givnish *et al.* (1984) on the basis of a cost-benefit model, carnivory could only evolve when the marginal benefit associated with carnivory (in term of increased photosynthesis or growth) exceeded the marginal cost (in term of carbon or biomass needed for trap construction as structural cost of carnivory). The model has become the fundamental platform underlying ecophysiological research on CPs since its origin (see Ellison & Gotelli 2001, 2009; Ellison 2006; Ellison & Adamec 2011; Pavlovič & Saganová 2015). Knight (1992) supplemented the model and

hypothesized that CPs invest a greater metabolic (energetic) cost in their traps as an increased dark respiration rate because the traps are physiologically more active than leaves. This maintenance cost was investigated for a variety of CP species with different types of traps and was confirmed for mobile traps (Adamec 2006, 2010a,b; Pavlovič *et al.* 2007, 2009; Hájek & Adamec 2010). Traps usually represent not only higher metabolic cost than leaves, but simultaneously also higher photosynthetic cost due to their specialization for carnivory as trap photosynthetic rate per unit DW is usually (much) lower than that of leaves (cf. Knight 1992; Adamec 2006, 2010a,b; Pavlovič *et al.* 2007, 2009; Hájek & Adamec 2010).

Moreover, traps of CPs usually contain a high proportion of total plant amount of growth-limiting mineral nutrients N, P, K, Ca, and Mg. Therefore, Adamec (2010c) postulated mineral cost of carnivory as the total nutrient amount in all traps which could also be expressed in percent of total plant nutrient amount. In aquatic CP species, mineral cost of carnivory for N, P, K, and Ca could extend even 60%. Although a great proportion of trap N, P, and K is reutilized from senescent traps, a part of them and all Ca and Mg are lost in senescent traps (Adamec 2002, 2011, 2014). Adamec (2010c) thus suggested a concept of mineral cost-benefit relationships which maximize mineral nutrient uptake from prey per minimal nutrient (N, P) losses invested into carnivory. This concept does not deny the above classic model (Givnish *et al.* 1984) proposed for terrestrial CPs but rather supplements it, as it specifies mineral nutrient economy of CPs after which carnivory is beneficial for the plants. Quantitatively, Adamec (2011) expressed the efficiency of mineral nutrient investment in traps (termed "total nutritional benefit of carnivory") as a ratio between the total amount of nutrients (N, P, K, Ca, Mg) coming from carnivory (either directly from prey or indirectly *via* stimulated root uptake) and that amount of nutrients lost in senescent traps over their lifespan. When this value for a given nutrient exceeds 1, carnivory will be ecologically beneficial. However, this nutritional model to date has received much less attention.

A marked stimulation of growth is commonly the final benefit of carnivory with significant ecological consequences. Givnish *et al.* (1984) predicted that carnivory would evolve among plants when the marginal photosynthetic benefits of carnivory exceeded its marginal costs. As foliar N and P contents in terrestrial CPs are low and photosynthesis commonly increases in well-fed CPs relative to starved ones (for review see Pavlovič & Saganová 2015), the low growth rates of CPs are at least partially limited by a shortage of mineral nutrients. So far, the stimulation of photosynthesis by prey capture has been confirmed in *Drosera capensis* (Pavlovič *et al.* 2014), 10 *Sarracenia* species (Farnsworth & Ellison 2008), *Nepenthes talangensis* (Pavlovič *et al.* 2009) and *N. alata* (He & Zain 2012) but some results are non-significant (Méndez & Karlsson 1999; Kruse *et al.* 2014). In *N. talangensis*, photosynthetic rate also rose after mineral enrichment of the soil (Pavlovič *et al.* 2010; cf. results for *Darlingtonia californica*; Ellison & Farnsworth 2005). On the contrary, the stimulation of photosynthesis in aquatic CPs by prey capture is quite ambiguous (Adamec 2008).

In feeding experiments in various terrestrial CP species, a marked growth increase in fed plants (usually 1.5-5 times) was observed (Adamec 1997, 2011) and it is therefore probable that the predicted increase in the specific foliar photosynthetic rate (per unit biomass) is very common in most of terrestrial CP species. Even if the specific foliar photosynthetic rate remains unchanged after prey capturing, another additional mechanism could ensure attaining of higher growth rate. In aquatic *Utricularia* species, prey capture can reduce significantly the proportion of traps to the total plant biomass (Adamec 2011, 2015). This reduction of structural investment in carnivory should consequently not only decrease the energetic cost of traps but also photosynthetic cost of shoots (*sensu* Knight 1992). The higher proportion of photosynthetically active leaves (over the traps) should ensure an increase of total plant photosynthetic rate as the photosynthetic benefit and, there-

fore, also of increased plant growth rate as the growth benefit, even if the specific photosynthetic foliar rate is not increased (Adamec 2008).

If the principal reason for the growth stimulation is the uptake of relatively small amounts of mineral nutrients N, P, and K from prey, using a functional-ecological approach, it is possible to express the plant growth increase due to prey capture or feeding *per amount* of N or P or K absorbed from prey (or a mineral solution applied onto the traps) in greenhouse or field-growth experiments. This model of growth benefit from carnivory shows the efficiency of biomass production per unit nutrient amount gained from prey. The "growth benefit efficiency" (GBE) of carnivory is defined as a ratio between a measured growth increase of CPs (*minus* unfed controls; in mg DW of the biomass) and a model amount of N, P, and K (in mg) gained theoretically from prey (or a nutrient solution) in published growth experiments. As shown in Table 1, the data on measured growth increase and weight of arthropod prey captured (or volume of a nutrient solution applied) could be drawn from 11 studies for 13 CP species. The model efficiency used for the uptake of N from prey was 40% (field) or 76% (greenhouse) and 90% for P and K, but 100% uptake of the nutrients in the case of nutrient solution (see Adamec 2002, 2011). Unless specified directly in the given study, the following mean nutrient contents in dry insects were taken into account (in % DW): N, 10; P, 1.0; K, 1.2 (Adamec 1997, 2011). As different kinds of arthropod prey as well as the efficiencies of nutrient uptake from these preys can differ considerably from the model values in different CP species or under experimental conditions, it is possible to assume that the true amounts of N, P, and K gained could vary from the model values at most by 30-40%. Thus, the calculated model GBE values in Table 1 could be loaded at most by a 30-40% error. Based on usual values of shoot or foliar nutrient contents (% DW; N, 1.0-1.5; P, 0.08-0.12; K, 0.8-1.5; Ellison & Adamec 2011) in CPs, the values of the GBE far exceeding ca. 70-100 for N, 800-1200 for P, and 70-120 for K can indicate an increase of specific photosynthetic rate per unit foliar DW. In contrast, the GBE in control non-fed plants is zero.

Results and Discussion

The calculated GBE (in mg/mg) for 13 CP species was between 21-5020 for N, for P between 206-13,000, and for K 170-10,400 (Table 1). What can be drawn from the data? The data show that the GBE can greatly vary for a given nutrient not only among different taxa, but also within the same species in different experiments or at different feeding levels (cf. *D. capillaris*, *D. aliciae*, *D. rotundifolia*, *P. vulgaris*, and *S. purpurea*). In *S. purpurea* overfed on prey, the GBE was by two orders of magnitude lower than that in this species naturally catching prey. It indicates that the efficiency is greatly reduced by high prey amount. The very high GBE values in two experiments on application of nutrient solutions onto the leaves (Adamec *et al.* 1992; Adamec 2002) may partly reflect relatively long duration of these experiments (7 and 4 months, respectively), during which the growth effect is amplified. Very high values of the GBE above the theoretical threshold (>100 for N, >1200 for P, >120 for K) indicate that the prey-derived uptake of the given nutrient is either relatively low to cover the increased growth (it could particularly apply for K as arthropods are relatively poor K source; the growth increase is mainly due to the N and P uptake from prey), or that the specific foliar photosynthetic rate is stimulated by the nutrient uptake. If all GBE values for N, P, and K are increased above the threshold, it directly indicates photosynthetic stimulation and, simultaneously, a possibility of the stimulation of root nutrient uptake (Table 1). This was proven for several *Drosera* species and *S. purpurea*, but neither for *P. vulgaris* nor aquatic *Aldrovanda vesiculosa* (cf. Méndez & Karlsson 1999; Adamec 2008; Farnsworth & Ellison 2008; Pavlovič *et al.* 2014).

Table 1. The comparison of experimental growth increase of CPs (*minus* unfed controls) by foliar prey feeding or natural prey capture or by application of a mineral nutrient solution (NS) onto the traps from literature data. This growth benefit from carnivory shows the efficiency of biomass production per unit nutrient amount gained theoretically from prey. The values shown in denominator in italics denote the efficiency of the total accumulation of the given mineral nutrient applied onto the trap. For detailed model assumptions see the text. Based on usual values of shoot or foliar nutrient contents, values far exceeding ca. 70-100 for N, 800-1200 for P, and 70-120 for K (in bold) can indicate an increase of specific photosynthetic rate per unit foliar DW. AQ, aquarium; GR, greenhouse; FI, field. 1: Adamec (2002); 2: Adamec *et al.* (1992); 3: Chandler & Anderson (1976); 4: Karlsson & Pate (1992); 5: Krafft & Handel (1991); 6: Thum (1988); 7: Thum (1989); 8: Aldenius *et al.* (1983); 9: Karlsson & Carlsson (1984); 10: Chapin & Pastor (1995); 11: Adamec *et al.* (2010).

Species	Growth condit.	Growth period (d)	Nutrient applic.	Biomass increase (DW) per amount of nutrients absorbed (mg/mg)			Comment	Refer.
				N	P	K		
D. capillaris	GR	125	NS	**702**/*14.4*	**2045**/*0.67*	**1948**/*25.1*	Droplets of NS	1
D. aliciae	GR	125	NS	**741**/*7.9*	**2158**/*0.87*	**2056**/*27.2*	-“”-	1
D. spatulata	GR	95	NS	**659**/*8.7*	**1920**/*0.85*	**1828**/*21.1*	-“”-	1
D. adelae	AQ	217	NS	**5018**	**13,128**	**10,406**	-“”-	2
D. aliciae	AQ	217	NS	**1298**	**3398**	**2693**	-“”-	2
D. capillaris	AQ	217	NS	**3062**	**8009**	**6349**	-“”-	2
D. whittakeri	GR	75-87	Flies	24.3-49.7	206-419	171-349		3
D. closterostigma	GR	121	Collemb.	**242**	**1345**	**1121**	Perennial species	4
D. glanduligera	FI	77	Flies	69.5	309	**258**	Annual species	4
D. rotundifolia	GR	2 seas.	Flies	56.3-69.0	313-384	**261-320**	5 or 10 flies/week	5
D. filiformis	GR	2 seas.	Flies	51.2-97.0	284-546	**237-455**	5 to 20 flies/week	5
D. rotundifolia	FI	162	Flies	**250**	1110	**834**	Corrected for	6,7
D. intermedia	FI	104	Flies	**171**	760	**571**	robbing prey	6,7
P. vulgaris	GR	45	Insects	21.3-26.6	94.6-118	78.8-98.4	Nutrient-fed peat	8
P. vulgaris	GR	47	NS	27.3	577	--	N or P application	9
P. vulgaris	GR	47	NS	68.5	377	--	N+P application	9
S. purpurea	FI	110	Nat. prey	**202**	**2024**	**1687**		10
S. purpurea	FI	110	Flies	1.37	11.0	10.4	Plants overfed	10
A. vesiculosa	GR	11	Zoopl.	39.4	372	29.6	Fed on ostracods	11

Conclusions

The GBE parameter defined in this study expresses the production of extra dry biomass per unit of N, P, and K taken up directly from prey but it tells nothing about the efficiency of the stimulation of mineral nutrient uptake by roots by foliar nutrient uptake and *vice versa* – both efficiency

parameters are independent of each other. This fact also follows from the data (Table 1). A direct measurement of foliar photosynthetic rate and the stimulation of root nutrient uptake by the foliar uptake are very demanding and costly. However, in growth experiments, an exact estimation of the growth increase as the growth benefit of carnivory and the DW of applied prey bodies for calculation of the growth benefit efficiency is relatively simple.

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Carnivorous plants exhibit a unique tropism

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Certain genera of carnivorous plants exhibit a tropism unique in plants. When liquid or solid protein is gently placed on the surface of the traps without stimulating the receptors for movement, the area around the object begins to move towards it. A name is proposed for this unique tropism.

Plants are known to move towards certain stimuli (water, light, gravity) which are beneficial and these movements have been labeled hydrotropism, phototropism, geotropism.

Three genera of carnivorous plants are well known for their rapid movements in capturing prey. The Venus' flytrap (*Dionaea muscipula*), waterwheel (*Aldrovanda vesiculosa*), and bladderworts (*Utricularia*, about 240 species) employ a mechanical trap.

Two other genera, *Drosera* (more than 230 species) and butterworts (*Pinguicula*, more than 100 species), ensnare prey with tiny sticky tentacles which, upon stimulation, bend towards the captive. If a tiny piece of meat or a drop of meat broth is placed on the traps without triggering movement, the tissues around the object begins move towards it, accompanied by the production of enzymes around the area. If broth or meat is placed on the leaves outside the trap, this reaction does not occur. This is also the case with *Dionaea.*

Although this phenomenon has been known for over a century (Darwin 1875; Lloyd 1942), this reaction by the plants as such has not been recognized as a tropism. I propose that this unique reaction be considered as a tropism unique to these genera and that it be named carnitropism.

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Keywords: cultivar, *Sarracenia* 'Mega Mouth', *Sarracenia* 'Monks Head Hammerhead', *Sarracenia* 'Red Beret', *Sarracenia* 'Tower of Terror', *Drosera belezeana* 'Dr. Frankensnyder's Monster'.

Sarracenia 'Monks Head Hammerhead'

Submitted: 4 June 2017

Sarracenia 'Monks Head Hammerhead' is apparently the 3rd or 4th generational offspring of *Sarracenia* 'Hummer's Hammerhead'. The plants and leaves of *S.* 'Monks Head Hammerhead' are larger in stature compared to the original parent. Leaves are 5-8 cm taller in height, hoods are 2-5 cm wider and are deeply approximated over the entire orifice or pitcher opening at top (Fig. 1). Coloration is very similar if not identical to the parent(s) *S.* 'Hummer's Hammerhead'. Early Spring leaves hold true throughout the entire growing season. Flowers have deep maroon red petals, again, very similar to the parent(s). In brief, *Sarracenia* 'Monks Head Hammerhead' is a form of the Hammerhead that has a general resemblance, though strikingly different in aspects.

The name is based on the long and wide hood overlapping the orifice of the pitcher, and its morphologic connection (parentage) to *S.* 'Hummer's Hammerhead'.

The plant has a vigorous growth habit, and is also a good "divider". It can only be replicated through plant division.

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Figure 1: *Sarracenia* 'Monks Head Hammerhead' growing in standing water Summer 2015.

Sarracenia 'Mega Mouth'

Submitted: 8 December 2016

Sarracenia 'Mega Mouth' is a hybrid of (*S. leucophylla* × *mitchelliana*) which I made in the spring of 2010 and selected in 2014.

Let us just start by saying that this incredible pitcher plant borders on the ridiculous. It is not only huge in proportions, but beautiful as well. Picture if you will the most colorful and vibrant *S. mitchelliana* on super steroids and you have *S.* 'Mega Mouth'. Mature spring pitchers average 60 cm tall with a mouth opening around 7.5 cm. Colors are green overlaid with the biggest and brightest white areolae from the tip of the lid (operculum) extending to every part of the pitcher inside and out for the top 1/3 of the trap with brilliant pink and red, thick, non-bleeding veins (Fig. 2). The hood is large and ruffled, approximately 10-12.5 cm wide from side to side and front to back. The peristome is rich pink and red.

Pitchers are formed during the entire season, but come to fruition in late summer. It is at this time that the spectacle begins. What is to follow is nothing short of amazing. Like its parent *S. leucophylla*, the best, biggest, and most colorful traps are made during the months of late August through September. These new pitchers, under my desert-like growing conditions, reach 50 cm tall with a mouth opening ranging from 7.5 to 12.5 cm across. Yes folks, that is 5 inches! The biggest of these are so big that they have been tested in person by several of my closest colleagues to swallow a 16 × 8 cm cell phone in its entirety. Flying insects have no problem flying in and out with ease. Due to the lack of prey capture in these extra-large traps, I do supplement with liquid fertilizer in the pitchers. The flowers are very large and a beautiful dark red. Phyllodia are produced year-round along with the functional traps. They too are very large, averaging 30-40 cm long by 5-7.5 cm wide.

Propagation must be done via division and cuttings in order to maintain this plant's unique features. This cultivar's epithet was coined in the summer of 2014 and refers entirely to its giant, gaping mouth.

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Figure 2: *Sarracenia* 'Mega Mouth' summer traps pitchers.

Submitted: 8 December 2016

Sarracenia 'Tower of Terror' is a hybrid cross between two cultivars, *S.* 'Leah Wilkerson' × *S.* 'Royal Ruby', which I made in the spring of 2008 and selected in 2014.

This incredibly beautiful pitcher plant is a mighty grower with adult pitchers standing at 75-85 cm or larger if grown in high humidity and intense sunlight. Pitchers start out green flushed with red, then mature into a deep red with faint greenish yellow areolae extending from the outer base of the peristome downward some 5 cm (Fig. 3). The beautifully fluted mouth is somewhat teardrop shaped giving it a yawning appearance and is just slightly smaller than the lid (operculum).

The lids, the crowning glory of this gem, are approximately 10-12.5 cm wide from side to side and from the front to back. Ruffled and flat; they do not curve upwards. The colors are astounding. There is a brilliant green strip that runs down the center of the lid from the base to the tip, flanked on both sides with strips of intensely brilliant golden yellow. Veins are deep maroon and form an elegant picotee around the outer edge of the lid. When viewed in direct sunlight the lids sparkle as if they are made out of gold. The color and effect is surreal. Pitchers are produced all season, but are at their largest early. Flowers are large and yellow.

Overall, the color combinations and elegant growth habit of this plant are so striking to the eye that one can see them gleaming in the sunlight from a distance.

Propagation must be done via division and cuttings in order to maintain this plant's unique features. This cultivar's epithet was coined during the summer of 2015 in reference to the amusement park ride – tall with a sheer drop. Only in this case, there is no stopping before hitting bottom.

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Figure 3: *Sarracenia* 'Tower of Terror' pitchers and top of lid.

Sarracenia 'Red Beret'

Submitted: 13 April 2017

In the summer of 2015, I received a batch seedlings from a supposedly open-pollinated *Sarracenia oreophila* × *flava* from a fellow Colorado grower. Among these, one particular specimen took off, reaching maturity within a couple of months and sending off several side shoots without slowing down. This plant showed clear signs of the red-lidded *S. alata* var. *rubrioperculata* in its parentage through growth pattern, color, and later flowers. Consequently, my best guess is that the parents are *Sarracenia* (*oreophila* × *flava*) × *alata* var. *rubrioperculata*.

Sarracenia 'Red Beret' is a vigorous, stout plant, pitchers reaching 60 cm tall and tapered from top to bottom in a gradual narrowing to produce a solid trumpet shape, sometimes bolstered by a thick wing on the front (Fig. 4). The slightest hint of a bulging top comes through from the *S. alata* parent, and the lid is broad and spade shaped, held out over the mouth with the sides curving back down the neck of the pitcher. The color is striking, pure lime to yellow-green on the outside with the dense reticulation of the veins from the pitcher interior just barely showing through, set off by the distinct deep red shade of the underside of the lid. This coloration halts in a near-perfect line at the junction between lid and neck, only extending downward in a narrow stripe through the center of the throat, and it never bleeds out, producing a crisp, clean-cut appearance. Flowers are large, up to 8 cm across with pale cream-yellow teardrop petals that splay outward at maturity.

In 2016, the name 'Red Beret' was suggested by another grower (Angie Hall) and fit perfectly. 'Red Beret' is a name reminiscent of military standing, calling attention to the crisp, precise coloration and rigid standing of this cultivar when in full growth; all pitchers at attention with their lids tilted ever so slightly up in salutation. Even the flowers are obedient with petals pointed rigidly down and at an angle once unfurled. This cultivar is suitable only for vegetative reproduction, either via division of growth crowns or by rhizome cuttings.

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Figure 4: *Sarracenia* 'Red Beret', front and rear views showing the pure green outer color of the pitchers and crisp red, non-bleeding color of the lid.

Drosera belezeana 'Dr. Frankensnyder's Monster'

Submitted: 14 July 2017

Drosera belezeana 'Dr. Frankensnyder's Monster' is a fertile tetraploid of the hybrid between *D. intermedia* and *D. rotundifolia*. The plant is named after Ivan Snyder and this is his story (pers. comm. 2017):

> The origin of our cultivar is quite an epic. It begins with an intriguing tale of possible natural amphiploid genesis. Jason [Ksepka] told me of his finding a great swarm of hybrids in [Burlington Co.,] New Jersey. He was trying to explain the concentration of hybrids found at one spot without the parent species presence. Might some of the plants at the swarm's center be reproducing from seed, or were they all just clones of a few extraordinarily vigorous sterile plants multiplying vegetatively. Jason actually found seed! He sent me some of this seed along with a clone of the plant which had produced them. The seed did indeed look intermediate between the parents; but refused to germinate. Jason felt he may have picked them prematurely. [He has not found any seeds since.]
>
> I continued to study the plant Jason sent me. Judging cell size, I determined the plant was diploid and thus the common sterile hybrid. It proved to be a good grower, although did not look at all special. This one individual natural hybrid Jason sent me received a boost in evolution. It responded very well to colchicine treatment. Leaf size increased beyond normal and it retained the great vigor it showed in nature. Unfortunately, I was unable to ever get the plant to flower for me indoors in Southern California. I gave the plant to Warren [Auyong] who then passed it on to John [Brittnacher]. Under John's care the plant flowered for the first time since becoming tetraploid.

Drosera belezeana 'Dr. Frankensnyder's Monster' more closely resembles its *D. rotundifolia* parent while the popular sterile cultivar *D.* 'Nightmare' (D'Amato 2013, p. 171) with the same parentage and from the same general location, resembles a very robust *D. intermedia* with more upright

Figure 5: Comparison of *Drosera belezeana* 'Dr. Frankensnyder's Monster' plants (left) and *D.* 'Nightmare' (right). The images are approximately at the same scale.

Figure 6: Comparison of *Drosera belezeana* 'Dr. Frankensnyder's Monster' flowers (center) with the parents, *D. intermedia* (left) and *D. rotundifolia* (right). The images are not to scale.

leaves and longer petioles (Figs. 5 & 6). *Drosera belezeana* 'Dr. Frankensnyder's Monster' may be propagated by leaf cuttings and seeds.

Some of the information about *D.* 'Nightmare' in D'Amato (2013) is incorrect. Jim Bockowski named and distributed *D.* 'Nightmare'. The original plant was from Burlington County, New Jersey, not Toms River (Bockowski, pers. comm. 2017).

Reference

D'Amato, P. 2013. The Savage Garden. Ten Speed Press, Berkeley, California, USA.

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